

# THE ALL-SUFFICIENCY OF NATURAL SELECTION.

A REPLY TO HERBERT SPENCER.

## I.

THE following essay is written as an answer to two articles by Herbert Spencer, one of which, "The Inadequacy of Natural Selection," appeared in the CONTEMPORARY REVIEW in February and March of this year, and is directed chiefly against my views on heredity and natural selection; while the other was published in May, as a "postscript" to the first, and is entitled, "Professor Weismann's Theories." I am never willing to enter into controversy, when the only object is to show others to be in the wrong; but I do so in this instance, as an opportunity is afforded me of expressing opinions on the subject of natural selection that I have long desired to make public, and for the utterance of which I might not otherwise have found occasion so soon.

Any one who has carefully studied the development of the problem of heredity in the course of the last ten years knows that my view of the intransmissibility of acquired characters has not yet received general assent and recognition among scientists. Many still believe that such transmission can be proved; and not a year passes without some "convincing" instances being published. Most of these depend on imperfect comprehension of what is to be understood by an "acquired" character; not a few, however, seem at first sight to be really conclusive against my view.

Among the latter I reckon, for example, the observations which Mr. Buckman, an English geologist, published last year.\* It is well-known that the little toe of our foot is more or less deformed: not only small, but curved; and this is commonly ascribed to the boot-pressure to which it is subjected during the greater part of our life;

\* S. S. Buckman, "Some Laws of Heredity, and their Application to Man," in *Proceed. Cotterwold Naturalists' Field Club*, vol. x, part iii, p. 252, 1902.

while it is assumed that the injurious effect of the pressure is inherited. This would be transmission of an acquired character. Yet it was possible to reply that perhaps the deformity of the toe arose in the course of each individual life, and was thus always acquired anew—an explanation which would appear to receive support from the circumstance that the little toe of our new-born children lies quite straight. Buckman has now, however, observed in the case of his own children, that the toe becomes curved, even if the children wear no boots, but go barefoot; and this happens as early as six months after birth. He concludes from this, quite rightly, that curvature of the little toe is *inherited*, and he believes that he has thus furnished an illustration of the transmission of acquired characters: he entertains no doubt that the deformity of the toe is due to boot-pressure.

This assumption, however, is erroneous. We have a very exact anatomical and statistical study of the little toe by W. Pfitzner,\* from which it appears that *it is undergoing a slow process of degeneration, which cannot be ascribed to boot-pressure*:† it is on the point of changing from a three-jointed to a two-jointed toe. Among forty-seven feet examined at the Strassburg Anatomical Institute, thirteen cases of synostosis of the second and third phalanges of the little toe occurred; and Pfitzner was able to demonstrate the same fusion of the joint in children under seven years of age, and in certain cases even in embryos. His researches were not at all meant to solve the difficulty as to the transmission of acquired characters; he seems, indeed, not even to have known that any such difficulty existed, for he quite ingenuously examines whether the cumulative effects of heredity could have aggregated the very slight atrophy of the toe that might possibly be produced by boot-pressure in individual cases. He negatives this question on the ground that the Japanese and negroes, who go barefoot, exhibit similar fusion of the phalanges.‡

At my request Professor Wiedersheim was kind enough to investigate the little toe of several Egyptian mummies; and it appeared that among these, too, the fusion of the phalanges could be demonstrated, and not only among adults, but also in the case of children.

So the matter is in much the same position as the degeneration of the tail of the dog and the cat, which likewise has given occasion for misrepresentation as dependent on the transmission of mutilations. Both organs are undergoing a very slowly increasing degeneration, the explanation of which in the case of the little toe offers even less difficulty than in that of the tail of the domestic dog; for physiology has long shown that the little toe, if of use at all, is of quite insignifi-

\* W. Pfitzner, "Die kleine Zehe": *Archiv f. Anatomie u. Physiologie*, 1890. P. 12.

† For the reasons why this explanation is inadmissible, see the original treatise. They chiefly turn on the nature of the change, which is such that it could not have been originated by pressure from the side.

‡ The same fact has recently been demonstrated by Martin in the case of certain Patagonians.

cant value in walking ; that it is thus superfluous—at least in its full original development, as still seen among the higher apes. But superfluous parts are no longer controlled by natural selection, are not preserved at the height of their development, but slowly sink through Panmixia. The hereditary degeneration of the little toe is thus quite simply explained from my standpoint.

I will not, however, pause to refute other apparent proofs of the transmission of acquired characters ; even were I to refute all that have hitherto been advanced, new ones would assuredly constantly be forthcoming ; and so, arguing in this way, we should hardly come to a conclusion. Besides, I have ever contended that the acceptance of a principle of explanation is justified, if it can be shown that without it certain facts are inexplicable. I have therefore ever made it my task to show that the assumption of the transmission of acquired characters is not necessary for the explanation of known phenomena ; and I have begun to render intelligible, apart from this belief, a large number of facts that have usually hitherto been only explained with its aid—*e.g.*, the degeneration of parts that have become superfluous, the development of instincts, and the existence of artistic talents in man. But I never for a moment doubted that all was not thus achieved, that there were other facts which apparently could not be explained without this assumption ; and among these was that one which Herbert Spencer \* has now brought to the front again in his essay in this REVIEW, holding it to be a decisive reason for belief in the transmission of acquired characters—namely, *the harmonious variation of the different parts that co-operate to produce one physiological result* [co-adaptation].

It is not for the first time that the distinguished author of the “Principles of Biology” brings forward this difficulty in opposition to my views ; seven years ago he published an essay† founded on essentially the same arguments ; and I should willingly have replied at that time, had I not been hindered by the prosecution of other studies. Having for many years been troubled by my eyes, I cannot carry on two pieces of work at once.

The following is a summary of Herbert Spencer’s argument : If a transmission of acquired characters does not occur, then all enduring variations must rest on natural selection ; but again, most, if not all useful variations of any one part must be connected with variations of other parts, if they are to be in any degree effective ; and often these co-operative changes are so numerous that it is difficult to understand how all, at one time and independently, should possibly arise through spontaneous variations and natural selection. We cannot believe, on the other hand, that all vary together ; that, for instance, the

\* Herbert Spencer, “The Inadequacy of Natural Selection”: CONTEMPORARY REVIEW for February and March, 1893.

† “The Factors of Organic Evolution”: *Kosmos*, 1886, p. 241.



enlargement of the antlers of the stag is always necessarily connected with a thickening of the skull and a strengthening of the neck ligament and the muscles of the neck and back; for we know numerous examples which prove that co-operating parts undergo quite distinct, even opposing, variations. How, if it were otherwise, could the great differences between the fore and hind feet of the kangaroo appear; or how could the powerful nippers of the common lobster arise on the pair of limbs that in the rock lobster bear simple little claws; and so on? One must then, Mr. Spencer thinks, believe that the co-operative parts vary independently of one another. But if this be assumed, then the process of change becomes not only protracted and complicated to an unlimited degree, but simply impossible; for how should all the co-operating parts offer at the same time suitable variations to be preserved by natural selection? Yet the enlargement of the antlers, for instance, requires a simultaneous strengthening of the ligament and the muscles that support the more heavily burdened head; even the processes of the dorsal vertebræ must vary in conformity with the increase; and so must the bones, muscles, ligaments, nerves, and vessels of all these parts, and of the whole anterior extremity. Can these hundreds of individual parts be supposed, independently of one another and simultaneously, to be modified in due proportion, and preserved by natural selection? But if they do not vary *simultaneously* then the variation of individual parts is of no avail; a strengthening of the muscles and ligaments of the neck, without an increase of the antlers avails nothing, and an increase of the antlers unaccompanied by a strengthening of the ligaments, muscles, &c., would be dangerous and highly disadvantageous.

There is thus no apparent alternative but to believe with Mr. Spencer that functional variations are transmitted, and that in this way all co-operative parts remain in harmony; *i.e.*, the variation of *one* part,—as, for instance, the antlers—is always accompanied by an exactly proportionate variation of the others, so far as is beneficial for the general efficiency of the parts. If this be so, belief in the transmission of acquired characters is unavoidable; and Herbert Spencer is so thoroughly convinced of the strength of his argument that he goes the length of saying: “Either there has been inheritance of acquired characters, or there has been no evolution.”

I am of a different opinion. Since I expressed the belief ten years ago, that functional variations (acquired characters) could not be transmitted, I have not ceased to test that view, and whenever I have been able to get a more thorough understanding of the facts, I have found it confirmed. But I freely grant that Mr. Spencer's objection is a tempting one; and I should not be surprised if many who read his essay, and are familiar with the enormous difficulties, which, according to his view, stand in the way of an explanation of the facts in question



through natural selection, should be carried away by the strength of his skilful representation, and hold the *easier* explanation of the facts—by the inheritance of acquired characters—to be the *correct* one.

I hope to show, however, that it *cannot* be the correct one, and that we must, here, as in the case of the degeneration of disused parts, set aside the apparently simple and almost matter-of-course explanation, and seek another.

What is simpler and more obvious than that organs which are not used degenerate, just because they are inactive? We know that activity invigorates muscles and many other parts, while inactivity renders them weak and thin; for a full explanation, then, we only need to assume that this deterioration is transmitted from generation to generation! Assuredly this idea is simple, but it is wrong. It is plainly contradicted by the fact that parts that are only *passively* functional, that is, such as are useful through their mere presence, as, for instance, the skin and skin-armature of crabs and insects, or the protective colouring of insects, degenerate likewise from the moment they become useless.

If it were possible to show that variations of a complicated structure, whose activities are dependent on many other “co-operating parts,” have proceeded without the possibility of the transmission of acquired characters coming into play, then there would be evidence that this last bulwark of the Lamarckian principle is untenable. And there are such cases, as it seems to me.

It fortunately happens that there are animal forms which do not reproduce themselves, but are always propagated anew by parents which are unlike them. These animals, which thus cannot transmit anything, have nevertheless varied in the past, have suffered the loss of parts that were useless, and have increased and altered others; and the metamorphoses have at times been very important, demanding the variation of many parts of the body, inasmuch as many parts must adjust themselves so as to be in harmony with them.

I refer to the neuters of the state-forming insects, especially the ants and termites. Among the latter there are usually two kinds of these, soldiers and workers: among the ants, as a rule, there are only the so-called workers. Every one knows that these “neuters” do not commonly propagate; their organs of reproduction remain small, and in most of the forms that have been fully investigated can be said to be quite rudimentary. But though they do not propagate, or do so only exceptionally, they yet differ from their parents, the males and females, more or less markedly in other parts of the body besides the reproductive organs, and these differences have increased and multiplied in the course of time.

This fact did not escape Charles Darwin, though he did not bear it in mind in dealing with the question which occupies us now. In

the "Origin of Species" there is a lengthy discussion of the origin of the neuter ants; and the explanation there given must still be regarded as the only possible one—namely, that they arose through selection of the parents. Darwin's endeavour was to defend the doctrine of evolution and the theory of selection against all possible objections, and to set aside the obvious difficulties; and as such an "apparently insuperable difficulty" he discussed the existence of neuters in the insect states. He accounted for their origin by supposing that a selection of the fruitful females must have taken place, inasmuch as females which produced sterile offspring in addition to fruitful issue were of special value to the state; for the existence of members that were *workers* only was a gain to it and strengthened it, and assured it a superiority over other colonies that had no workers. So in course of time the states with workers conquered those with none, and in the end caused them to disappear. In the same way all the variations among the workers arose, to make them more fit to be of service to the state.

It may be difficult to think out such a slow and indirect selection; but we must nevertheless hold this explanation to be correct, as it is the only possible one, unless, indeed, an inner developmental force is assumed to originate the metamorphosis of organisms, as by Nägeli and others. I long ago, however, produced ample evidence\* that such a "phyletic developmental force" is contradicted by innumerable facts. It would only be reconcilable with the very exact adaptation of all organisms to their conditions of life, by the assumption at the same time of a "pre-established harmony" between the life-conditions and the nature of the metamorphosis, so that every tiniest change in the former would be quite exactly limited as to time and place, and would correspond to a hair's breadth with the similarly limited variations in the organism. Leibnitz, as is well known, conceived body and soul to be related in this way, and compared them to two clocks so constructed as always to go exactly alike, though independent of one another.

Such a hypothesis would not suit the author of the "Principles of Biology"; and as he, moreover, recognises the efficiency of natural selection, he will require no other explanation of the occurrence of the neuters than the Darwinian, unless he would seek to contest the facts—to which I shall return. But, as soon as he has recognised this explanation to be the right one, he will have granted, at the same time, that not only degeneration of parts, but even the harmonious and efficacious metamorphosis of many co-operative parts can proceed without any concurrence of the transmission of acquired characters.

\* "Studien zur Descendenztheorie," Leipzig, 1876, pp. 295 and 322: Eng. trans., "Studies in the Theory of Descent," part iii., London, 1882, pp. 664 and 706.

I proceed now to the proof. The ants are animals whose life and doings, as well as their organism, have been most minutely investigated. A long list of excellent observers have thought them worthy of prolonged research; and many of these, as, for instance, P. Huber, A. Forel, and the Jesuit Father Wasmann, have devoted their lives, giving all their time and all their energy, to them. We have, then, such a large store of admirable information concerning the ants that our theoretical conclusions regarding them can be founded on a firm foundation; and for this reason I leave the termites, as to which our information is much less certain and exact, altogether out of account.

That the *ant-workers* have arisen through phyletic metamorphosis of fruitful females may well be taken for granted, without explicit proof. What other origin could they have had? And this is the view taken by all recent investigators from Forel to Wasmann. To this day there are some species (e.g., *Leptothorax acervorum*) in which the workers closely resemble the females, and in the same species, forms intermediate between the females and workers have frequently been found. Wasmann\* established no fewer than six different categories of such transition forms. As to the *nature of the modifications* which distinguish the workers and females, they are partly *retrogressive*, partly *progressive* or dependent on a fuller development of certain parts.

*Retrogression* in the ovaries and receptaculum seminis is found among the workers of all the species of ant that have been examined. We are indebted to the researches of a Swedish naturalist, Adlerz, for exact information on this subject; and from his work it appears that the receptaculum has completely disappeared in all the species studied by him, and that the ovaries have degenerated in various degrees: in one species twelve egg-tubes persist in each ovary, in another only one to five, in a third only three, in others only one or two; in *Tapinoma* and almost all the *Myrmicida* there is only one, while in *Tetramorium* there are none at all.

Retrogression is also found in the *eyes of the workers* of many species. The three ocelli are often wanting altogether; and the number of facets in the compound eyes, and, as a consequence, the quality of the eyes, is more or less reduced, compared with that of the males and females of the same species. Forel has given us the results of many exact observations on these relations; for instance: the male of *Formica pratensis* has about 1200 facets in each eye, the female of the same species has only 830, but the worker has only some 600; again, the male of the common turf-ant, *Solenopsis fugax*, has more than 400 facets, the female about 200, while the worker has only 6-9.

\* E. Wasmann, "Ueber die verschiedenen Zwischenformen von Weibchen und Arbeitern bei Ameisen"; *Stettiner Entomolog. Zeitung*, 1890, p. 300.



That the males should have the most highly developed eyes cannot surprise us, as we know that this is very often the case among insects; there are even species of Ephemerids (*Potamanthus*) in which the male, in addition to the common compound eyes, has others quite distinct, large and turban-shaped, on the top of its head, so that it has a very peculiar appearance. The truth is, it is the males that seek out the females, and therefore their better sight is of advantage to them during the nuptial flight high up in the air. The females, too, use their eyes during the flight; and it is only the workers, which always live and labour on the ground, and largely, even, in dark places, that are restricted to a limited use of their organs of vision.

But perhaps some will doubt whether there is here an actual degeneration in the workers and not simply a higher development of the compound eyes of the males and females. I hold it to be quite possible that in certain cases the compound eyes of the males and females have increased since the institution of a worker type; but that reduction has, at the same time, taken place in the workers' eyes is proved not only by the disappearance of the ocelli in many species, but by cases like that of *Solenopsis fugax*; for the females of no living species in which a nuptial flight occurs have eyes composed of so few as only 6-9 facets, and accordingly the ancestors of the ants must have had large compound eyes, like all predatory hymenoptera that have not become state-formers.

Again there has been retrogression in the wings of the workers, and so complete that there is no appearance of them in the perfect insect. But in this case, too, it can be proved that the ancestral forms possessed wings; for Dewitz has demonstrated the imaginal discs of the wings in the larva, though they develop no further in the pupa.

Besides the wings, the two segments of the thorax on which the wings are situated, as well as the muscles of the thorax which move the wings, have degenerated in the workers. The latter point has been directly established by Adlerz in the case of *Camponotus* and *Formica*, but could also be inferred from the marked reduction of the two posterior thoracic segments. These segments are, at the same time, much more simply constructed than in the males and females; the ridges which bound the small shield-shaped areas of the mesothorax, the so-called scutellum and pro-scutellum, are wanting altogether, and so is the post-scutellum, while the two little side-pieces, which lie under the usual position of insertion of the posterior wings, are fused. The changes in the thorax are thus just such as would necessarily arise through transmission of the deteriorating effects of disuse, if there were any such inheritance. *But the workers are sterile, and can transmit nothing at all.*

Likewise rudimentary among the workers are all the instincts which are concerned with reproduction.

I have elsewhere attempted to show that all these degenerations in the sterile members of the state-forming insects can only be explained by Panmixia, as where there are no heirs there can be no transmission of the effects of disuse. Moreover, a degeneration of the wings cannot be accounted for by transmission of the consequences of disuse, even if the workers had progeny; for the wings of insects are passive organs, whose perfection in no way depends on their being employed; they are complete before they are used, and are rather injured by wear than strengthened by use. I long ago\* pointed out other similar cases (skin-armature of hermit-crabs, &c.), and can only explain Mr. Spencer's ignoring such cogent instances by supposing that, as a philosopher, he is unacquainted with the facts by personal observation, and that therefore they appear less weighty to him than to a naturalist; for I would not for a moment suppose that he purposely evades the difficulties which face his opinion, as is the manner of popular orators and advocates—and alas! even of some scientists.

It is the ants, too, that suggest another interesting case, which proves that degeneration of an organ does not depend on the transmission of functional atrophy, but that there may be degeneration of an organ even when it continues to function. The reduction in the number of facets in the eyes of the workers would not be referable to the transmission of functional atrophy, even if the workers reproduced themselves, for their eyes are not much less exposed to the light than in earlier days when they were fertile females. We have not to do with animals that live in absolute darkness, but alternately in the light and in the dark, just like the females, which are similarly situated except as regards the nuptial flight. The eyes of the workers are thus in fact not out of use; they are exposed to the light nearly as much as those of the females, and can therefore certainly not fail through lack of function. But they degenerate *because, and in so far as, they are superfluous for the full performance of the tasks of a worker*; so, in this way again, we are led to Panmixia.

The second group of variations which have appeared among the workers are progressive developments of certain parts; and, above all, the great increase in the brain has to be named. This is connected with the higher intelligence and manifold instincts of the workers, whose functions, as is well known, are of varied nature and partly of a kind that could only exist through the formation of states and the existence of a working-class. But even externally the workers are not infrequently distinguished by peculiarities which are closely connected with their activity, and so cannot have been transmitted from the sexual forms, and in course of time lost by these. Among these characteristics are, for instance, the long thorns which the workers of some species (*e.g.*, *Atta*) have on the head and back.

In *Atta*, too, the workers are distinguished from the females by yet

\* "Aufsätze über Vererbung," u. s. w., p. 571, English trans., vol. ii. p. 20.

more evident marks. In certain species two forms of workers occur, one of which, because they undertake the defence of the colony, are usually called "soldiers," and these are often very different from the other workers, and still more from the females. Thus, in *Pheidole megacephala* the head of the soldiers is much larger, and is equipped with far more powerful jaws, and the size of the head allows the muscles which move the jaws to be of quite unusual dimensions, as Lubbock, who has studied the life of this South-European species,\* points out.

In the Mid-European species, *Colobopsis truncata*, Emery has also discovered two worker-forms, and the "soldiers" in this case are so distinct from the common workers that they had previously been held to be a different species (*C. fuscipes*) when they were found in the nest of *Colobopsis truncata*. Here again the soldiers have a large and thick head, which they make use of in a very peculiar way. It is so large that it just fills up one of the many little approaches to the nest, and so the soldiers keep guard, each of them holding possession of a doorway.

It can hardly be gainsaid that we have here variations in which, in lesser degree, processes must be involved similar to those Herbert Spencer has justly assumed in the case where the head of a stag (e.g., the Irish elk) is loaded with ever larger and heavier antlers; that is to say, *many parts must have varied simultaneously and in harmony with one another*. If the jaws became stronger and larger, they could only continue to be useful provided the muscles that move them became stronger, and if the chitinous capsule of the head, to which they are attached, became thicker. The head must thus have become larger, and the cuticle thicker at the same time; likewise the nerves which supply the masticatory muscles must have become richer in fibres, so as to be able to supply all of the much more numerous muscle-fibres; and in a corresponding degree the appropriate motor-centres in the brain must have undergone an increase of their elements, and so on. Yet with all this we are not done; for as in the stag the heavier horns required a strengthening of the ligaments, bones, and muscles of at least the neck and anterior extremities, so the larger and heavier head of the ants that have been metamorphosed into soldiers could no longer have been supported and moved by the thorax and limbs, if there had not been an increase in the firmness of the skeleton and in the joint-membranes, muscles, and nerves of these parts.

None of these changes can rest on the transmission of functional variations, as the workers do not at all, or only exceptionally, reproduce; they can thus only have arisen by a selection of the parent ants dependent on the fact that those parents which produced

\* Sir John Lubbock, "Ants, Bees and Wasps."



the best workers had always the best prospect of the persistence of their colony. No other explanation is conceivable; *and it is just because no other explanation is conceivable, that it is necessary for us to accept the principle of natural selection.* It alone can explain the adaptations of organisms without assuming the help of a principle of design. Mr. Spencer complains bitterly that in my essays the words, "it is easy to imagine" are frequently used; and thinks many of my arguments are based on things "easy to imagine." Perhaps the expression is blameworthy, in so far as it permits conclusions to be drawn from inadequate evidence; but I am glad to be able to say that I have really not used it, at least not in the way complained of by Mr. Spencer. My opponent has overlooked the fact that the English edition of my Essays is not the original, but a translation. The expression "it is easy to imagine" is not mine at all, but is a somewhat too free translation of various phrases in the original German. The passage specially referred to by Mr. Spencer reads thus in the German edition (p. 92): "so könnte man immerhin daran denken dass . . . ;" which is not at all so matter-of-course as "it is easy to imagine" implies; and a translation faithful to the meaning, if not very elegant English, would read somewhat as follows: "one could perhaps even think to explain this by assuming . . . ." In another passage ("Aufsatz," VIII. p. 525) the "it is easy to imagine" rests on the words: "es ist also an und für sich durchaus nicht unzulässig"; in a third ("Aufsatz," IV. p. 235) there is: "allein es wäre ja ganz wohl denkbar"; and out of the eight places in which the expression occurs\* in the English edition, there are only two in which it stands likewise in the German, and my severe critic will assuredly have nothing to say against its use in these. On page 156 of the first English edition, these words occur: "In all these cases it is easy to imagine the operation of natural selection in producing such alterations in the duration of life . . . ."; and on page 430: "we can easily imagine how it happened, when we learn that tailless cats are especially prized in Japan. . . . ." I think a naturalist may well endeavour to conceive in concrete form facts which he has inferred; there is even a certain degree of confirmation of what has been merely inferred, when it is possible to form a conception of it that goes into details. The truth of the inference does not, indeed, depend on our being able to do this, but follows from the convincing strength of the deduction,—naturalist and philosopher are at one as to this, *in theory*, at least.

It seems to me, though, that *in practice* my opponent is almost

\* One of my friends has taken the trouble to look through the English edition of my Essays for the expression "it is easy to imagine." He did not find it in Essays I., V., VI., VII., IX., X., XI., and XII.; it occurs twice in II., once in III.; in IV. the word "imagine" appears three times in a somewhat different connection; and "easy to imagine" is also twice in VIII.

more disposed than I to justify assumptions by the ease with which they can be imagined. He sets aside the possibility of explaining complicated harmonious metamorphoses of the body (co-adaptations) by natural selection, because such varied and involved contemporaneous processes of selection cannot be imagined; but, on the other hand, he assumes the extraordinary height of the giraffe's body to be due to natural selection, because here the process appears easy to imagine. The truth is, he is compelled to this assumption in the second case, because the Lamarckian principle of the transmission of functional variations fails him; for as he says, a lengthening of the leg and neck through stretching up for high twigs cannot be suggested.

I must say that, in respect of warrant to assume the process of natural selection, it does not seem to matter much whether we can easily, or with difficulty, or only with great difficulty, imagine it; and for this reason, that I do not believe that we are in any case able to conceive in detail the actual morphological metamorphoses concerned. I, too, refer the length of the neck and forelimbs of the giraffe to processes of selection; but I contend that we can only conceive these quite generally and very indefinitely. There are no data for a fuller conception; we know neither how great must be the changes which are able to decide for life or extinction; nor do we know how often variations occur to be accumulated by selection; nor even how often, at what intervals of time, they result in selection. We know, indeed, nothing at all but the chief foundation of the process; and therefore any one who does not comprehend the logical necessity of the theory, or will not recognise it, can easily set aside the individual instances as untenable. Herbert Spencer seems not to know that Nägeli \* in a book that attracted much attention among scientists ten years ago, analysed this very case of the giraffe, and attempted to show that processes of selection could by no means explain the height of the giraffe.

My opponent thinks further that the extraordinary delicacy of the tip of the tongue cannot be explained by processes of selection, and that I would certainly not contend that any person ever succumbed in the struggle for existence because he had a less sensitive tongue-tip than others. Such a result, apparently, seems to Mr. Spencer difficult to imagine. And it is so, because we see only very imperfectly into the life-struggle of animals, and still more because we so readily forget that in such highly developed organs as the tongue of man we have to do with the final result of an endless perfecting process, which has been going on through thousands and thousands of species, a process which, again, we are quite incapable of representing to

\* "Mechanisch-physiologische Theorie der Abstammungslehre." München u. Leipzig, 1884.

ourselves at all adequately. Our imagination does not grasp such immense successions of time and such long-protracted lines of development; we speak of them without rightly knowing what we say, pretty much as when we talk of billions or trillions; we must reduce the immense multitude to a unity to be able to work with it, for the multiplicity exceeds our experience too far; and that is easily forgotten. Moreover, in many animals, and, indeed, in those that are most nearly related to man, the apes—as Romanes\* has already very rightly pointed out in reply to Spencer—the tongue is an organ of touch, and has not only to function in the mouth, moving the food during chewing, but serves at the same time as a hand, and is used for the examination of external substances. Why then should there not be a decided advantage in the struggle for existence to those individuals in which it is more delicately constructed than in the others of the same species. The life of animals necessarily depends on the acuteness of their sense-organs.

But, truly, in this case there is refuge for the followers of Lamarck in the transmission of acquired characters, provided it can be assumed that the touch papillæ of the tip of the tongue have ever increased in number through much use. There are examples enough, however, in which it is possible to exclude this hypothetical factor, and I should like to adduce one of these, which has long seemed to me to be a good proof of how little depends, in the assumption of processes of selection, on whether we can readily or with difficulty conceive them.

Very many insects, and particularly the bees and wasps, have on the lower end of the tibia of the anterior leg a slightly movable spur-shaped process, and opposite this, on the metatarsus, there is a small, nearly crescent-shaped notch, which is beset with a comb of minute teeth; and this "strigil" serves for the cleansing of the antennæ, the part that is to be cleansed being drawn between the spur and the strigil, as if between the two blades of a pair of scissors. F. Dahl,† in particular, has investigated and figured this interesting and very delicate arrangement, as it is found in many insects; and Canestrini and Berlese‡ had written on it somewhat earlier.

The strigil, then, forms an abrupt and very striking interruption of the surface of the leg, and in one of the small bees, *Nomada*, has quite the appearance as if some one had struck out with a punch a crescent-shaped piece from the limb, so sudden and regular is the notch. It looks as if the insect, through ever and again drawing its antenna between spur and tarsus, had gradually produced this crescentic notch. But that would be to assume transmission of

\* Herbert Spencer on "Natural Selection" in CONTEMPORARY REVIEW, No. 823, April 1893, p. 499.

† F. Dahl, "Beiträge zur Kenntniss des Baues u. der Functionen der Insecten-beine." Berlin, 1884.

‡ Canestrini and Berlese, "La streggia degli Imenotheri." Padua, 1880.



acquired characters, which in this case is excluded by the fact that the function of the cuticular skeleton is purely passive. Insects have their legs fully formed when they leave the pupa, and, as they do not later undergo exuviation, there can be no suggestion of a functional variation of the chitinous skeleton, which is no longer a living part of the insect, but a derivative from the underlying layers of living cells. Even if the cleansing of the antennæ acts like a file, only dead substance will be removed, much as when we file down the finger-nails; and assuredly even the most stiff-necked believer in the transmission of acquired characters would hesitate to maintain that such a defect could be transmitted.

As this explanation is not possible, then, there remains only that of natural selection. It is again "easy to imagine" that it must be of advantage for the insect to be able to free such important sense-organs as the antennæ from dust and dirt; but, as soon as the attempt is made to think out the process in detail, we recognise that here, too, we know nothing thoroughly, and that it would be uncommonly easy for any one who wished to assign the processes of natural selection altogether to the realm of phantasy to emphasise this view; for *it is really very difficult to imagine this process of natural selection in its details*; and to this day it is impossible to demonstrate it in any one point. As a sudden origin of the strigil is excluded, we should have to assume that the notch began, in some members of the species, by the appearance of a small depression of the strongly convex surface of the metatarsus at the site of the future strigil, and that, in the struggle for existence, these individuals had thereby an advantage over others. How easy, however, would it be for an opponent to doubt this superiority. He might, perhaps, be ready to believe that an insect which has no means of cleansing its antennæ would be at a disadvantage compared with another which has such means, but he would say that it was absurd to believe that so trifling an improvement in the cleansing apparatus as is represented by a slight depression of the tarsus could be decisive as to which should succumb and which survive.

Dozens of similar objections have been raised against the occurrence of natural selection, and not by ignorant and superficial thinkers only, but by very learned and thoughtful men of science: I need only instance Nägeli once more. We cannot compel such an antagonist to take our view, at least not as regards any single instance, for we cannot prove that which he doubts: we are unable to show by direct evidence that such a small advantage can turn the balance in favour of life or death; and much less that it must do so in many cases, and in generation after generation, till finally the variety with a shallow depression is the dominant one. All that we can do is to show the utility of the perfected arrangement, by removing, as Forel did, the

anterior tibia with the strigil from such an insect and establishing that very soon the antennæ become dirty, and the insect is no longer able to clean itself.

But though the process of natural selection, which we must insist on, *began* with the formation of a slight depression opposite the spur, it was very far from ending with that. How does it come about, our opponent will say, that the gradual deepening of the depression proceeds so regularly that at last a quite deep, crescent-shaped hole has arisen? Is it possible that only such variations were advantageous and decisive between life and death as exhibited perfectly regular progress from the initial depression to the final, well-cut semi-globular hollow? And how can it be believed that somewhat less regular deepenings, which must have occurred along with the regular ones, always, again and again, brought about the death of the insects in which they appeared? Lastly, the depression of the strigil is also beset with microscopic teeth: did every one of these, if they arose by chance variations, give the verdict between life and death, before becoming a fixed possession of the species?

To the first objection we could perhaps answer that the processes of natural selection are very protracted; and therefore the notch, which was perhaps irregular at first, may have become ever more regular in the course of untold generations, always because the strigil served its purpose so much better the more perfectly it fitted the form of the antenna that had to be cleansed. We might remark that the strigil of different living species is developed in very different degrees, and that, from its common occurrence among the insects, we may infer that it has been undergoing continual, slow improvement since the earliest days of insect life on the earth. But this, too, may make no impression on my adversary, who calmly continues to assert that such a tiny improvement could not give the decision for life or death. And the same is repeated in connection with the last objection, when, perhaps, the answer has been given that the teeth which clothe the strigil have arisen, not individually, but all at once, at first as a slight roughness of the chitinous surface, then as ever more prominently projecting and more regularly formed points.

Just as in this instance, so is it in every individual case of natural selection. We cannot demonstrate any of them, and there is no use attempting to make them seem unanswerable by having recourse to the co-adaptation which Mr. Spencer brings forward. Moreover, I believe there are hardly any metamorphoses which do not involve the harmonious variation of *several* parts, in the production of a useful structure. It is so in the case of the strigil, for the spur of the tibia which is opposite the excavation in the metatarsus forms the other limb of the scissors through which the antennæ are drawn during the cleansing process; and it, too, by its free movement and by

its peculiar situations, is exactly suited to its function. So selection must have affected it, also; for here again, *variation because of function is excluded*, as the spur is only *passive* in its function. It is true the results of artificial selection are in favour of the occurrence of natural selection, but as Herbert Spencer justly observes, the two processes, though they may be analogous, are certainly not identical. The struggle for existence plays the part of breeder in the case of natural selection; and how this factor works we are unable to determine in any single case. Who would say of any little variation in the form of any existing species that it is sufficient to give its possessor the victory in the struggle for existence, and so may become the starting-point of an advantageous metamorphosis of the part? Even in the simplest of cases that is impossible; no one, for instance, could decide how much the colour of a green insect must vary, so as to originate a process of selection dependent, perhaps, on adaptation to a new and somewhat differently coloured fodder-plant. We cannot estimate what Romanes has recently very well called the "selection-value"\* of variations, which Lloyd Morgan had previously spoken of as the "elimination value"; we can only say generally with Darwin that selection works by the accumulation of very slight variations, *and conclude from this that these "slight variations" must possess selection-value*. To determine accurately the degree of this selection-value in individual cases, is, however, as yet impossible.

So when any one asks with Herbert Spencer: Do you believe that a little *plus* of perceptiveness in the tip of the tongue has ever been decisive as to who shall perish and who survive? one may reply in the affirmative, and another in the negative, with equal right; for one finds it easy, the other difficult, to imagine; and neither of these judgments is convincing.

The question might also be put: Do you believe that when the eggs of a bird whose surroundings are grey acquire a faint grey tint the victory is thereby secured over the original white? To that many nowadays would assuredly answer Yes; but some would as certainly say No; and in my opinion both would be wrong, for how should we know the selection-value of these variations?

But let us go on to ask: Do you believe that a variety of robber-fly with *one* facet more in the compound eye than the other members of the species have, will from that derive so great advantage that it will leave behind it more descendants than the others; or must there

\* In physiological variations it is somewhat different, though even here numerical values cannot be given. If, for instance, some plants of a southern species withstand the frosts of winter, while most succumb to them, we have an indication of selection-value; but we know nothing of the structural changes, except their effects and their utility for the northward-pressing colony of the species. That the species is, because of these changes, able to spread northwards is not implied, but depends on many other factors.



be *two* facets more ; or would selection-value only be attained by a difference of *ten* ? Who is able to say that he can affirm anything on the subject ? And yet, apart from natural selection we have no explanation of the wonderfully exact adaptation of the compound eyes of all insects to their life-conditions.

Thus we could ask questions for ever without getting a definite answer. But let me put one more, which will lead us back to our consideration of the ants : Do you believe that the fine bristles on the broad metatarsus of the honey-bee have arisen because slight variations of the female bees, leading up to this result, have been of so great value as to secure the survival of the hive over others ? The answer of many will be that this is not only *difficult* to imagine, but that it is quite incredible, seeing that the workers have themselves no advantage from the change, and do not live longer, or better on account of it ; and that it only enables them to carry a little more pollen at a time to the hive, and to feed the bee larvæ a little more abundantly or quickly, which could not possibly be decisive for the extinction or survival of this family of bees in competition with other families. If one realises that the workers are sterile, and that, accordingly, not they themselves, but their parents, the sexual bees, must have been the subjects of selection dependent on whether they brought forth better or worse workers, then it becomes quite unthinkable that such tiny variations as the slight broadening of the metatarsus, or a denser coating of bristles on it, could ever have given the verdict for or against the continuance of the parent-bees.

I am, of course, not of this opinion, but believe that here, as in the case of the ants, every little improvement in the workers proceeds from the variation of a determinant of the germ-plasm that was contained in the germ-cells of the parents. For fuller explanation I would venture to trust to the theory set forth in my recently published book.\* According to it the dimorphism or polymorphism of a species is represented in the germ-plasm by the doubling or multiplying of certain determinants, while it depends on certain conditions, which are for the most part unknown to us, which of the representative determinants or groups of determinants become active, and which remain passive. By "determinants" I mean units of the germ-plasm that are the primary constituents of definite cells or groups of cells of the body. When, now, corresponding parts appear in two forms in any species ; when, for instance, the scales of a certain part of the wing of a species of butterfly are brown in the female, but blue in the male, this is provided for in the germ-plasm, according to my view, by the determinants of the wing-scales occurring doubled, one set representing the primary constituents of brown scales, the other of blue. Both cannot become active in the same individual—*i e.*, cannot

\* "The Germ-Plasm : A Theory of Heredity." London : 1893.

lead to the formation of scales, but while one set remains inactive the other is destined for activity.

So when, instead of dimorphism, there is polymorphism, when, for instance, the females of a species are similarly distinguished among themselves, and occur in two forms, this results, according to my idea, from the double determinants becoming triple determinants. If there were workers among the butterflies, and if these showed red colour on the part of the wing that is blue in the male and brown in the female, there would always be three representative determinants present at a definite part of the extremely elaborate and highly complicated germ-plasm; but only one of these would become active during the development of the egg or sperm-cell concerned, and would produce the patch of brown or blue or red scales on the wing.

According to this theoretical representation, every part of the body of the bee or ant that is differently formed in the males, females, and workers is represented in the germ-plasm by three corresponding determinants, but on the development of an egg, never more than one of these attains to value—*i.e.*, gives rise to the part of the body that is represented—and the others remain inactive.

Thus, then, the metamorphosis of the body-parts of the workers of ants and bees will have to be considered in connection with the fact that the males and females whose germ-plasm contains favourable variations of the determinants of the workers have a better prospect for the maintenance of their successors than others which show less favourable variations of such determinants. The process of selection is the same as if the matter at issue were the attainment of favourable adaptations in the body of the sexual forms; for in both cases it is, as I once before said, not really the body that is selected, but the germ-plasm from which the body develops. The difference is this: in the one case the survival in the struggle for existence depends on characters and variations of the body of the individual; in the other, only on the character of a certain kind of descendant—the worker. If the ant-state were composed of individuals connected together like a colony of polypes or *Siphonophoræ*, a process of selection by which only the workers were changed would be within easier reach of our imagination, as these would then, in a manner, be only *organs*, just like the snaring-threads, the swimming-bells, and the gastric tubes of the *Siphonophoræ*. As these do not reproduce, and accordingly can only vary by selection of the egg or germ-plasm from which the whole colony is formed, so in the case of the ant-colony, or rather state, the barren individuals or organs are metamorphosed only by selection of the germ-plasm from which the whole state proceeds. In respect of selection the whole state behaves as a single animal; the state is selected, not the single individuals; and the

various forms behave exactly like the parts of one individual in the course of ordinary selection.

From this point of view a circumstance that must otherwise appear unmeaning becomes intelligible, namely, *the limitation of the fertile females of a hive to a single one*, as is the case among the honey-bees. Were many females of a hive engaged at one time in the production of eggs, the natural selection that depends on the quality of the brood of workers brought forth would be far more difficult and much slower, inasmuch as the prosperity of the hive would depend on many differently constituted workers, and so, in some measure, only the resultant of the produce of all these females would be selected: a queen would by no means be doomed to extinction because she produced a bad race of workers, for her hive would at the same time be provided with a brood of workers by other queens, and if the majority of these produced better workers, the hive would perhaps hold their own against others in the struggle for existence for a long time, till at last the worsen worker-brood distinctly preponderated in the hive. Obviously the workers must be more rapidly improved when all in a hive are the progeny of one queen—*i.e.*, if they are all alike or almost alike. The hive would survive in the struggle for existence if this one queen produced better workers, if, consequently, the brood was more quickly and better cared for, if more provision were made for the winter, and so a lower mortality prevailed in the hive. I could almost suppose that the remarkable reduction of the fertile females to a few (termites) or only one (bees) has taken place because the gradual improvement of the sexless by natural selection can thus to some extent proceed more easily and more rapidly; or rather, the hives with few queens had an advantage, because they could improve themselves relatively more quickly. It seems to me that the selection of workers is "*easier to imagine*" in these circumstances, though truly only in principle and not in detail. As soon as an attempt is made to think out in detail the process of selection by which, perhaps, the little bristles or the small baskets of the worker-bees have arisen, it is seen that all and every one of the data are wanting. Moreover, in my opinion we cannot hope that we shall ever possess them, either in these cases or in any yet simpler process of natural selection. Not only would it be necessary to form an estimate of the smallest variations, so as to know whether and how often among 1000, 100,000, or millions of individuals there is a variation which gives verdict over life and death: but much more that we can never determine is required; for instance, the number of individuals of a species living at one time, the degree of their mingling with one another in their own domain, and the percentage occurrence of the variation in question. All which, I am convinced, cannot be ascertained; and so we shall never be able to establish by observation the progress of natural selection.



What is it then that nevertheless makes us believe in this progress as actual, and leads us to ascribe such extraordinary importance to it? Nothing but the power of logic; we must assume natural selection to be the principle of explanation of the metamorphoses, because all other apparent principles of explanation fail us, and it is inconceivable that there could be yet another capable of explaining the adaptations of organisms, *without assuming the help of a principle of design*. In other words, *it is the only conceivable natural explanation of organisms regarded as adaptations to conditions*.

Certainly one could not know *a priori* whether other factors did not take an important part in bringing about the metamorphosis of species, and till twenty-five years ago, I myself entertained the opinion that besides primary variations and their accumulation and arrangement by natural selection, the inherited results of use and disuse played a not unimportant part. It looks quite as if it were so, as Mr. Spencer very plainly shows by his illustrations of the harmonious metamorphosis of many and diverse co-operating parts proceeding parallel with use. But does it not seem to be true that unused parts degenerate directly because of disuse? And that is not so, as I think I formerly proved, and have now confirmed with facts. If the eyes of the workers of many species of ant degenerate, although the animals do not propagate, and though their eyes are hardly less exposed to the light than those of the sexual forms by which they are produced, the change *cannot possibly* depend on transmission of the effects of disuse. And if harmonious metamorphosis of the head and all its co-operating parts and those of the thorax has occurred among some of the sterile ant-workers, this must also have taken place without any co-operation of the hypothetical transmission of functional variations. Against this conclusion there is no resource: once the facts are established, there is no escape left.

Are then the facts disputable? That is the question that remains to be considered.

The supporters of the Lamarckian principle can urge that the sterility of the ant-workers is not absolute; that it has been proved that now and then they produce eggs, from which, though of course they remain unfertilised, males proceed; and that this is sufficient for the transmission of the characters of the mother-worker. The reply to which might be the following: It is true that in many species the workers occasionally produce eggs (Forel, Lubbock, Wasmann). This is especially the case when they are in confinement and under artificial conditions, particularly when the temperature is high; but it occurs, so far as we know, only exceptionally. But even if a small percentage of the males were to arise from such eggs, there could never be an equal distribution of the characters of the workers through the entire colony as a result; for the few males that are

produced by the workers have to contend with the far greater number of males produced by queens. If it were the case that all the males of the colony proceeded from the eggs of workers, and if the queens had only female offspring, the objection would indeed be justified; and then the ants could no longer serve as an illustration of the occurrence of metamorphosis of species in circumstances that precluded the possibility of the transmission of functional variations; but so far as our knowledge goes, the case is otherwise. I know, it is true, of no observation that directly demonstrates that the queens produce both males and females, as has long been established for the bees; but the opposite view—that the queens produce no males—is much further from being proved. If we recollect that even the bee-workers in certain circumstances produce eggs, from which, as among the ants, only males arise; and further reflect that the ovary has degenerated in very different degrees in the various species of ant, in *Solenopsis fugax*, for instance, all the egg-tubes having disappeared, so that *sterility is complete*; we shall be compelled to hold it to be extremely improbable that in any of the species the duty of producing males has devolved on the workers exclusively. Rather we shall have to take the view that in the course of the phylogenetic development of the workers, first there was diminution in fruitfulness, accompanied by disappearance of the *receptaculum seminis*—which implies that only unfertilised eggs could be produced; then this limited reproduction became rarer and rarer, while the number of egg-tubes continually declined; and at last in *Solenopsis fugax*, with the disappearance of the last egg-tube the fall-off in productiveness was complete. This agrees with the opinions of our best specialists; and Forel, in his great work on the ants of Switzerland, affirmed that *infertility was one of the essential characteristics of workers*, and that it was only because of this infertility that they had become more capable of performing the many tasks that now fall to their lot than the fertile females, which are burdened with many eggs.

If any hope is left to the Lamarckians that this mighty mass of evidence supplied by the ants can be got rid of, this is the point on which that hope must depend; and so I would meet in anticipation yet another attack. Forel has frequently observed that *old* ant-colonies contained only males; and the attempt might be made to infer from this that there had been only workers in the colony, and that these had produced the males. But the fact is capable of a much more natural explanation, if one remembers that the same is true of the bees: there are hives in which neither young workers nor queens are found, but only males (drones); and we know that these males are the offspring of a so-called “drone-breeding” queen—*i.e.*, of an old queen whose supply of sperms has been exhausted, and which accordingly is no longer able to fertilise the eggs which she lays. In

the case of the ants exactly the same will occur; and we know from Lubbock's observations that queen ants may live to be fifteen years of age, which gives time enough to exhaust the sperms in their receptacle.

It might, perhaps, be said that the workers had only lost their fertility late in the course of phylogeny, and after they had undergone the other metamorphoses. But this assumption is untenable, as both the bodily structure and the activities of the workers are closely connected with their unproductiveness. Forel holds strongly that the production of sterile individuals was the first stage in the development of the workers. According to his view, the working power of a state was first increased by the decline of fertility in a large number of the females, while, as a consequence, there was a constant improvement in strength, intelligence, and activity, and a gradual disappearance of parts that had become useless: of wings, because there was no longer a nuptial flight; and of ocelli and a part of the compound eye for the same reason.

It would be possible, moreover, to doubt the sufficiency of this argument, and yet believe sterility to have appeared after the other characters. In this case, at least *one* question would remain for the Lamarckians to answer: *how did the production of sterile forms come to be established as a hereditary arrangement?* Certainly not by transmission of functional variations; for this variation, sterility essentially excludes inheritance.

Moreover, there is another way to show that after the appearance of sterile workers new variations were still possible, and even such as involved the simultaneous change of many parts in harmony with one another. This is implied in the occurrence of certain *species with two kinds of workers*, one of which must have sprung from the other by gradual metamorphosis. I have spoken above of the soldiers of *Pheidole megacephala* and *Colobopsis truncata*, whose immense heads and jaws could only have arisen from the corresponding parts of the other workers by harmonious metamorphosis of many distinct parts.

But some will doubt whether the soldiers really have sprung from the other workers by gradual metamorphosis, and will perhaps say that they might as well have been directly derived from fertile females, and only have lost their fertility when the other changes were completed. Against this idea, however, we have the fact that many stages in the development of double worker-forms exist at the present day, and so enable us to infer the history of their origin. Some species exhibit slight differences in the size of the workers; in others the differences are markedly greater though the larger workers are still connected with the smaller by many of intermediate size; then there are species in which these connecting-links are wanting; and these lead to others in which, accompanying the increase in size, there are



other changes : in form and in instincts. The soldiers have thus not arisen independently of and simultaneously with the other workers, but have been formed in accordance with the principle of division of labour by further differentiation of already existing workers, that is to say, *at a time when the present sharp distinctions between females and workers had long been established, and the regular reproduction of the latter had long ceased.*

If any one still doubts that all the various metamorphoses of females to workers have come about independently of direct transmission, and so not according to the Lamarckian principle, I would refer him to a study of certain instincts of the ants, and their consequences as regards the organisation of the workers. By the custom, or rather instinct, to make and keep slaves most remarkable changes have appeared in the slave-holders; and these can only be explained by natural selection as the slave-making impulse must have arisen long after the formation of workers. Most species of ants make no slaves; but some species occasionally do, and at other times do not, as, for instance, the much discussed *Formica sanguinea*, which has been very carefully observed in many lands. In this species the workers often go forth to hunt; they break in upon a colony of another species (e.g., *F. pratensis*), and carry off the pupæ to their own nest. This instinct, however, is not yet a firm possession of the species, for there are colonies in which no slaves are found; so it may be assumed that slavery has been introduced in relatively recent times, and in accord with that view is the fact that in *Formica sanguinea* there have been no changes in structure and habit like those that appear in *Polyergus rufescens*, all the colonies of which contain slaves, and among which, accordingly, the slaving instinct has become a fixed specific character. Between these two phylogenetic stages—that of *Formica sanguinea* and that of *Polyergus rufescens*—lies the origin of the remarkable changes to which I have referred as resulting from the slaving-instinct in *Polyergus*, namely, *the metamorphosis of the jaws from useful tools to deadly weapons and very admirable transport apparatus, and the degeneration of the ordinary instincts of the workers.* All these must indisputably have come about without any co-operation of transmission of functional variations.

The jaws of *Polyergus rufescens* have lost the so-called chewing-edge. Ants do not really chew in the literal sense, but they lick; frequently, indeed, they use their jaws to tear their food to pieces; but the chief purposes for which the jaws are employed are connected with all manner of household work; they serve for the transport of eggs, larvæ and pupæ, hither and thither; for dragging building materials along; for the formation of passages, cells, and spaces in the nest; and for mining in wood or in the ground, &c. In *Polyergus* the workers have forgotten all such household instincts; they no longer

trouble themselves about their young, but leave them entirely to the care of slaves; they bring in neither food nor building materials, as the slaves sufficiently supply these; they do nothing but fight, and steal the pupæ of other species, and carry these away to their nests. Accordingly their jaws are metamorphosed to sabre-shaped, pointed and powerful nippers, which serve as a deadly weapon that the ant is wont to employ in piercing the heads of its enemies, and at the same time are remarkably well adapted for the transport of plundered pupæ, as the jaw-nippers can embrace the body of the pupa without injuring it. This exact adaptation of the jaws for the stealing of pupæ can only be explained by selection of the germ-plasm of the parents of the workers; and the same can be said of the strongly developed fighting-instinct, of the great courage displayed, and of the instinct that leads these ants to steal the pupæ of others, and carry them away to their nests. Here, then, we have *positive selection*.

On the other hand we have *negative selection* or Panmixia in the decline of the ordinary instincts of the workers: those that are concerned with care of the young, nest-building, the storing of food, while *most uncommon and most instructive of all is the degeneration of the instinct to search for food*.

Herbert Spencer in his essay likewise attacks Panmixia, and attempts to show that I mean by this name the selection of the less injurious, and that nothing can be explained by this. He considers my example of the blind cave animals (*e.g.*, *Proteus*), and gives it as his opinion that it is impossible that the principle of the economy of growth can here have given the verdict for life or death, inasmuch as the difference in the size of the eyes of the individual varieties must have been much too trifling. So far I agree with him thoroughly. But Panmixia is, according to my representation of it, something quite different from the survival of the least unsuitable; it is the deterioration of organs from the height of their development *through the non-disappearance of such individuals as possess them in less perfect form*. In my opinion all organs are maintained at the height of their development only through uninterrupted selection, and decline incessantly, though at the same time excessively slowly, as soon as they cease to be of value for the maintenance of the species. That is what I have called Panmixia, as Professor Romanes recently very properly pointed out in the reply to Mr. Spencer to which I have already referred. The principle of economy was only introduced by me as a possible secondary cause of degeneration. The words actually used in the case of the *Proteus* are these:

“Possibly accessory is the fact that smaller and degenerated eyes may now”—after the retrogression of the organ has begun—“even be advantageous, inasmuch as other organs which have become more important for the creature, such as the tactile and olfactory organs, may be all the more strongly developed. *But even apart from this*, the eye will necessarily decline

from the height of its development, slowly, very slowly indeed, especially at the beginning of the process—but *surely* from the moment it is no longer maintained at this height by natural selection. Similarly *all* cases of degeneration, whether of organs or species, may be explained in a simple manner.” \*

How far-reaching the principle of economy may be in certain cases of degeneration cannot easily be determined; but that my former opinion was correct, according to which *Panmixia alone* suffices to bring about the complete disappearance of characters, is proved, among other things, by the above-mentioned degeneration in the warlike amazon-ants (*Polyergus rufescens*) of the instinct to search for food. Not only the males and females, but the workers of these ants, have altogether forgotten how to recognise their food. Forel, Lubbock, and Wasmann have all satisfied themselves that Huber's old statements on this subject are correct, and I myself have repeated his and Forel's experiments with the same results. The animals starve in confinement, unless some of their slaves are present to feed them; they do not recognise a honey-drop as something that would appease their hunger, and when Wasmann placed a dead pupa between their jaws, they did not begin to eat, but at most licked it in a tentative way and withdrew. But as soon as a slave—for instance, a worker of *Formica pratensis*—is put beside them, they come to it and beg for food; and the slave runs to the honey, and having filled its crop, proceeds to feed its lords.

So it is not the feeding instinct that is wanting here, as has often been said, but rather the capacity to seek and recognise the food. To be exact: the instinct to take food is *not aroused by the sight of food, but by the sight of the slave*. It appears as if these amazons had through the constant presence of slaves that were ever ready to feed them, gradually lost the habit of seeking food, and at the same time had come to regard the slaves as food-providers. It seems an excellent example of the direct effects of disuse and the transmission of functional degeneration—if only these amazons were not sterile!

The one possible explanation is that of *Panmixia*. As the amazons, because of the constant presence of slaves, never suffered want, the perfection of the instinct to seek food ceased to be an element in deciding which should survive and which should perish. Individuals with badly developed feeding instinct were, *cæteris paribus*, quite as good as others; and colonies in which such individuals occurred did not decline sooner on that account. Thus this instinct must slowly have fallen from its original perfection, and finally, though assuredly after an immensely long series of generations, quite disappeared. I fully grant that this is very “difficult to imagine”; but it must have occurred, as all other explanations are excluded by the infertility of the amazons.

\* “Aufsätze,” pp. 568, 569.



We are unacquainted with the particulars of the material foundation of instincts, and do not know in what cells or fibres of the brain this instinct is situated, but be that as it may, there is no doubt that the saving of material substance consequent on the decline of the instinct is so trifling in amount that it is very improbable that the principle of economy has, in this case, played even an accessory part. So we have here an instance of *complete disappearance of a character, for the explanation of which we are compelled to turn to the principle of Panmixia.*

This is not the place to enter into details as to this principle of explanation, which is simply an inference from a general acceptance of the principle of selection as an efficient factor in all adaptations. Once it is admitted that the adaptations of parts are always due to selection, it follows from the occurrence of variation, itself the chief factor in selection, that they are also maintained by selection. For though a useful character must become all the more constant, the longer the period through which it has been confirmed by constantly repeated selection, yet observation proves that no character, however old it is, ever attains to perfect constancy; but always slight variations occur. Therefore, as soon as selection ceases to affect a character, it must slowly begin to decline from the stage of development already reached.

This consequence of selection was not propounded by me for the first time; but as we have recently learned, was urged ten years ago by Romanes;\* and if this acute investigator did not succeed in bringing his correct inference into favour with scientists, it was because he did not give up the transmission of acquired characters, which he still adheres to; thinking, like Spencer, that, having regard to the harmonious metamorphosis of co-operating parts (co-adaptation), it is not possible to dispense with the principle of the transmission of functional variations; and so he continues to regard me as an "ultra-Darwinian." But Romanes in 1874 made the cessation of selection only of subsidiary importance, supposing it to support other factors, especially "economy of growth" and "disuse," in bringing about the degeneration of disused parts. He says: "The cessation of selection should therefore be regarded as a reducing cause, which co-operates with other reducing causes in all cases, and which is of special importance as an accelerating agent, when the influence of the latter becomes feeble." But if, as he thinks, disuse is directly effective through the transmission of functional atrophy, and economy of growth also co-operates in the degeneration of organs, then it would be impossible to demonstrate the influence of the cessation of selection, inasmuch as its effects would necessarily always be mixed

\* *Nature*, vol. ix.: "Natural Selection and Dysteleology," in the number for 12th March, 1874; in the number for 9th April, 1874, a second article: "Rudimentary Organs"; and in the number for 2nd July, 1874, a third: "Disuse as a Reducing Cause in Species."

up with those of the other factors. If only Romanes had considered the workers of the state-building insects, he would have recognised that the factor whose influence he rightly inferred, can *unaided* bring about degeneration, that it is thus the *chief* factor. At the same time, however, this would necessarily have upset his conviction that there is transmission of functional variations; and he would not have concluded his article with the words: "However, as before remarked, the question thus raised is of no practical importance, since whether or not disuse is the principle cause of atrophy in species, there is no doubt that atrophy accompanies disuse."

Thus it happened that a conception that was fully justified could not find favour, and all but fell into oblivion. Romanes thought that disuse only partially explained degeneration, and that "cessation of selection" subsequently set in. So the difference in the reduction of the wings of ducks and geese, in spite of equal disuse, would be intelligible: the variations in the species having been correspondingly different. This quite agrees with my opinion, inasmuch as Panmixia must, in truth, depend, as regards the time of its activity, on the variability of the species concerned; and it is this that in such cases as that of duck and goose indicates that *disuse is not the true cause* of organs becoming rudimentary. Romanes was very near the truth, but did not reach it; he continues thus:

"I deem it in the last degree improbable that disuse should not have assisted in reducing the unused organs of our domestic animals, and the effect of this remark is to show that *the cessation of selection is not able to accomplish so much reduction as I antecedently expected*. On the other hand, it seems to me no less improbable that the cessation of selection should not have here operated to some extent; but in what degree the observable effects are to be attributed to this cause, and in what degree to disuse, I shall not pretend to suggest."

I myself was led to the discovery of the principle of Panmixia through serious doubt as to transmission of acquired characters. If there was no such transmission, then there must be another cause of the disappearance of useless parts to be discovered; and so I was led to Panmixia. When I was compelled to deny both the transmission of functional atrophy and the transmission of the effects of the principle of economy in the individual ontogeny, the new principle was at once demonstrated as active: there remained for me only the *one* explanation of organs becoming rudimentary, that of selection, either *negative* selection alone (Panmixia), or with the aid of *positive* selection, which prefers, and gives the victory to, the less injurious. Of course I can only speak of the principle of economy in this latter sense, which, moreover, was understood by Spencer, and not in the sense of a transmission of effects of the struggle of parts in the course of ontogeny. I would also specially emphasise the fact that after full consideration of the relations among the ants, I am more disposed, even, than ten years ago, to regard the principle of economy as a very

unimportant factor in reduction, and one which, in most instances, probably takes no part at all.

Assuming, now, that we have proved that the transmission of functional variations has had no share in producing the harmonious variations of many co-operating parts in the case of the ant-workers, we must consider with what right we may look upon natural selection as the active factor.

The answer is very simple: *with the same right as we have for believing in its activity anywhere else in nature.* As already indicated, we accept it, not because we are able to demonstrate the process in detail, not even because we can with more or less ease imagine it, but simply *because we must, because it is the only possible explanation* that we can conceive. For there are only two possible *a priori* explanations of adaptations for the naturalist—namely, the transmission of functional adaptations and natural selection; but as the first of these can be excluded, only the second remains. It has often been said that proof of the actual intervention of natural selection in the development of organisms has not yet been produced; we can readily imagine its occurrence, but there is no cogent reason for the belief. This is indeed true; but I think that proof, based on the relations among the ants, can be produced.

First, even without the help of this exceptionally favourable instance, it is possible to lead proof of probability. That natural selection is really an active factor, and that variation, heredity, and the struggle for existence—i.e., the decimation of progeny—actually produce the adaptations of organisms to their environment is not only rendered highly probable by the fact that all organisation is revealed as adaptation as soon as it is rightly understood, and that the three named factors are proved to be efficient, but the probability is greatly increased by our *knowledge of the artificial selection that is practised by man.* In this analogous process there are two factors, variation and heredity, just as in the assumed natural selection, and only the third factor is different.

The high theoretical value of artificial selection seems to me to consist in the assurance it gives us of the ascending and cumulative effects of the first two factors in natural selection. If we had had to do without this, it would have been difficult to prove natural selection; for our knowledge of the fundamental processes of variation and heredity is much too limited to enable us to anticipate the consequence on the offspring of the combination of similar or dissimilar parental characters. Artificial selection, however, has provided us with a rich store of experience, and *we may now confidently found on the fact that improvement and general variation in definite directions can come about through selection of parents that are specially suited for the breeder's purpose.*

This, however, is the foundation of the process of natural selection.



We know that changes in definite directions can be produced by selection, and it only remains to consider the third factor of the process, the one that regulates the selection; and this factor, the struggle for existence, happens to be one that leaves no doubt as to its general activity.

That there are variations which must lead to victory in the struggle for existence is beyond doubt, though we cannot recognise them as such in advance; the survival of the fittest is certain, but we do not know in individual cases what is fit, nor yet how often in every generation it survives, and must survive, if it is to gain the victory. We cannot then, as a rule, produce evidence that a particular adaptation has arisen by natural selection. But if, as in the case of the ants, the other possible explanation, that of the transmission of functional variation, can be excluded, *we have a demonstration, at least for the particular instance, of the actual occurrence of natural selection.*

And now we are justified in further concluding that if in this one definite but many-sided instance the struggle for existence acts as natural selection assumes it to act, that is, like the breeder who in artificial selection chooses what suits him, then *even the small variations which occur in all parts of the body may possess selection value*; and if that is so in this case, there is no reason why they should not in countless other analogous cases have the same significance; in other words, *natural selection effects all manner of adaptations.*

We are thus able to prove by exclusion the reality of natural selection, and once that is done, the general objections which are based on our inability to demonstrate selection-value in individual cases, must collapse, as being of no weight. Therefore I shall not attempt here to give an exhaustive explanation of harmonious variation. It does not matter whether I am able to do so or not, or whether I could do it well or ill; once it is established that natural selection is the only principle which has to be considered, it necessarily follows that the facts can be correctly explained by natural selection. The explanation may be difficult, and through lack of data it may be impossible to put it beyond doubt; but the fact is not thereby contradicted, just as the view of modern physiologists that there is no peculiar vital force is not negatived, though to this day we cannot explain even a single vital process by purely physical forces. I believe, however, that an approximate and general explanation of harmonious variation (co-adaptation) is now possible, and I shall elsewhere attempt to give such an exposition; but, whatever its defects may be, no evidence can be drawn from them in favour of the transmission of functional variations, which seems to me to be definitely discredited now that it has been ousted from its last lurking-place—the harmonious variation of co-operating parts. When it is remembered that direct proof of such transmission is wanting, and that accordingly the justification for its acceptance has rested only on its being apparently

indispensable for the explanation of certain facts, it must be admitted that now that it has been shown that these facts occur where transmission of functional variation is excluded, there is no longer any sufficient reason for assuming this principle of explanation in any other case. If the workers of an ant-state can change into "soldiers," and can vary a large number of co-operating parts harmoniously without any help from the supposed transmission of functional variations, then there is no reason why we should deny the same capability to the stag or the giraffe. It would be illogical to assume a new and unproved force in these cases, after the analogous metamorphoses in the ants have been shown to occur without any such force. To that Mr. Spencer must agree, for he says: "A recognised principle of reasoning—the law of parsimony—forbids the assumption of more causes than are needful for explanation of phenomena" (p. 750).

Accordingly I hold it to be demonstrated that all hereditary adaptation rests on natural selection, and that natural selection is the one great principle that enables organisms to conform, to a certain high degree, to their varying conditions, by constructing new adaptations out of old ones. It is not merely an accessory principle, which only comes into operation when the assumed transmission of functional variations fails; but it is the chief principle in the variation of organisms, and compared to it, the primary variation which is due to the direct action of external influences on the germ-plasm, is of very secondary importance. For, as I previously said, the organism is composed of adaptations, some of which are of recent date, some are older, some very old; but the influence of primary variations on the physiognomy of species has been slight and of subordinate importance. Therefore I hold the discovery of natural selection to be one of the most fundamental ever made in the field of biology, and one that is alone sufficient to immortalise the names of Charles Darwin and Alfred Wallace. When my opponents set me down as an ultra-Darwinist, who takes a one-sided and exaggerated view of the principle discovered by the great naturalist, perhaps that may make an impression on some of the timid souls who always act on the supposition that the *juste-milieu* is proper; but it seems to me that it is never possible to say *a priori* how far-reaching a principle of explanation is: it must be tried first; and to have made such a trial has been my offence or my merit. Only very gradually have I learned the full scope of the principle of selection; and certainly I have been led beyond Darwin's conclusions. Progress in science usually involves a struggle against deep-rooted prejudices: such was the belief in the transmission of acquired characters; and it is only now that it has fortunately been overcome that the full significance of natural selection can be discerned. Now, for the first time, consummation of the principle is possible; and so my work has not been to exaggerate, but to complete.

AUGUST WEISMANN.